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The Emerson effect: a new approach

by A.B. Milin and A.A. Sivash

We studied the effect of the enhancement of photosynthesis in some green, brown and red marine macroalgae. We used a model of the light curve with one and two photoreactions, and carried out a quantitative analysis of the initial nonlinearity of the photosynthetic light curve. In algae taken from different habitats varying in light conditions, we studied the effect of the nonlinearity of the initial segment of the light curve on the enhancement of photosynthesis. The observed effect can be fully attributed to the sigmoid nonlinearity of the photosynthetic light curve, and not to the unbalance of the two photosystems.

The Emerson effect (enhancement of photosynthesis, E), observed when two beams of different wavelengths interact, can be attributed to the necessity of the balanced functioning of two photosystems, PS I and PS II [4, 10]. The value of E depends on the ratio of the photosynthetic rates observed in each of the two beams, and it decreases with an increase in the intensity of generated light, which the authors attribute to the nonlinearity of the light characteristic of photosynthesis upon transition to saturation [12, 13]. At the same time, we have found that the nonlinearity (sigmoid nature of the initial segment of the photosynthetic light curve, PLC) greatly influences the value of E [11]. This sigmoid nature, which is determined by the decreased activity of the oxygen-evolving centres during low light intensity [5] or by the photostimulated absorption of O_2 (photorespiration) [8, 9], produces higher values of E in comparison with those observed without it [7]. The measured values of E in the segment of the light curve with minimal nonlinearity [10, 11] or on a relatively highly illuminated background [11] were significantly lower than the "usual" ones; however, the authors themselves do not believe that these approaches have made it possible to completely eliminate the effect of the sigmoid nature of the curve on the experimental value of E. The inaccuracy of this method is one more factor that makes it impossible to completely eliminate the effect of

nonlinearity by graphic "linearization" of the initial segment of the light curve, which greatly reduces the value of E (from 8 to 1-2) [4].

Therefore, despite the fact that the majority of authors investigating the effect of enhancement acknowledges that the nonlinearity of the photosynthetic light curve influences the Emerson effect, the question concerning the relative contribution of nonlinearity and unbalance of the photosystems to this effect is still unresolved. In this particular study, we have used models of photosynthetic light curves with one and two photoreactions [2] for quantitative determination of the initial nonlinearity of the light curve and its influence on the value of the enhancement effect being studied (E).

Method

In our experiment, we used marine macroalgae, namely green *Ulva fenestrata*, brown *Punctaria plantaginea* and red *Porphyra yezoensis*. The algae, taken from different habitats, were kept in a continuous-flow aquarium with a biological filter and continuous bubbling, at a water temperature of 18-20° C and illumination of 20 W/m^2 (ДРЛ 700 lamp). The rate of O_2 evolution was measured by the polarographic method [3] with seawater flowing through the cell (500 ml/h). Monochromatic light was obtained with the help of a diffraction monochromator with an incandescent lamp (24 W, 340 V) or interference light filters (maximum filtration at 704 and 636 nm, 683 and 564 nm; half-width of filtration band 12 and 14 nm) with an iodine lamp (24 W, 150 V). The Emerson effect was calculated on the basis of the P_1 and P_2 values of photosynthesis effected by two light beams with wavelengths of 704 and 650 nm and 683 and 564 nm respectively, with different intensities and ratios. The experiment was carried out in the following variants: 1 - the "usual" variant in which the ratio P_1/P_2 and rate $P_{1,2}$ were varied by changing one of the values (P_1) while keeping the other (P_2) constant [2-9]; 2 - the rates of P_1, P_2 and $P_{1,2}$ were varied by proportionally changing P_1 and P_2 simultaneously while keeping their ratio constant; 3 - the ratio P_1/P_2 was varied while keeping the total $P_{1,2}$ constant. The values of the effects of enhancement E_1 and E_2 were calculated by the standard formulas [2]:

$$E_1=\frac{P_{1,2}-P_2}{P_1},\ E_1=\frac{P_{1,2}-P_1}{P_2}.$$

where E_1 and E_2 denote the effects of enhancement for the 1st and 2nd beams respectively, $P_{1,2}$ is the total level of photosynthesis effected by both beams, and P_1 and P_2 denote the level of photosynthesis for the 1st and 2nd beams respectively. The relative quantum efficiency of photosynthesis was calculated by the formula:

$$\varphi=\frac{V}{A\cdot J};\ V=\frac{P}{P_{max}},$$

where $A\cdot J$ denotes the intensity of absorbed light in quanta, and V the relative rate of photosynthesis.

Results and Discussion

The enhancement curves E_1 and E_2, derived by the usual method (variant 1), are similar to those for other organisms [6, 11], i.e. the value of E_1 decreases, while E_2 initially increases, but then diminishes with an increase in the rate of photosynthesis, which is consistent with the description in the literature. The decrease in E_1 is attributed to an increase in the unbalance of the photosystems, while the presence of a peak on curve E_2 is attributed to the balancing out of the photosystems [4, 10, 11]. Analysis of the form of the photosynthetic light curves shows that they are characterized by a nonlinearity of the initial segment ($P<0.3\ P_{max}$), which manifests itself in a decrease of photosynthetic efficiency with a low rate of photosynthesis (Fig. 1). A comparison of the curves derived in the 2nd variant of the experiment (Fig. 2) shows that the peaks of E_1 and E_2 are in the nonlinearity region of the light curve, and that the values of E_1 and E_2 approximate 1 (no enhancement) on the linear segment of the light curve (with $P>0.3\ P_{max}$) when photosynthetic efficiency is at its highest. This fact causes us to question the above interpretation of the form of the E_1 and E_2 curves.

In order to simulate the effects of enhancement, we used a model of a photosynthetic light curve with one and two photoreactions [2]. An estimation of the sigmoid nonlinearity of the light curve has shown that the values of E_1 and E_2, measured with an invariable intensity ratio of the two monochromatic beams "1" and "2" in the region of this nonlinearity, are significantly higher than those which result from the

unbalance of the photosystems (true effect of enhancement). The true effect of enhancement is observed when the base maximum value is attained through quantum efficiency. In the absence of enhancement due to unbalance of the photosystems, the values of E_1 and E_2 measured in the region of sigmoid nonlinearity are also significantly greater than 1, and approximate 1.1-1.2 on the linear segment, but never exactly 1, due to the "residual" effect of the initial nonlinearity (Fig. 2).

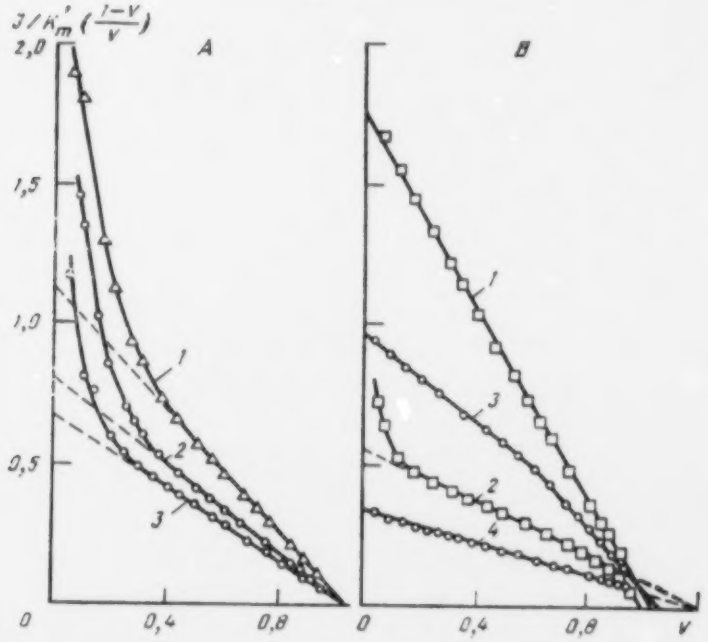

Fig. 1. Photosynthetic light curves for marine macroalgae in linearizing cooridinates (A): 1 - *Punctaria plantaginea* (light excitation with λ=564 nm); 2 - *Ulva fenestrata* (λ=704 nm); 3 - *Ulva fenestrata* (λ=636 nm). Photosynthetic light curves of *Porphyra yezoensis* from different habitats in linearizing coordinates (B): 1, 2 - from a darkened place (cavern); 1, 3 - light excitation with λ=683 nm; 3, 4 - from illuminated shallows; 2, 4 - light excitation with λ=564 nm

The experimental photosynthetic light curves for *Porphyra yezoensis* from different habitats have shown that a sigmoid nonlinearity is found only in algae from a darkened place (cavern) with λ=564 (Fig. 1, B, curve 2). At the same time, nonlinearily is not observed in the case of light excitation with λ=683 nm. In algae taken from an open shallow area, nonlinearity is not observed on the initial segment of the light curve under the effect of light with λ=564 nm or λ=683 nm (Fig.

1, B, curves 3, 4). The experimental curves of dependence of E_1 and E_2 on $P_{1,2}$ for the photosynthetic light correlation with both a relatively high degree of sigmoid nonlinearity (Fig. 1, A, curve 2), and a low one (Fig. 1, B, curve 2) are similar in form to the model ones in which the entire enhancement effect is determined by sigmoid nonlinearity. This attests to the fact that, in this case, enhancement of photosynthesis due to unbalance of the photosystems does not exist (or is very insignificant). In the presence of sigmoid nonlinearity during light excitation with λ=564 nm (Fig. 1, A, curve 2), the enhancement effect diminishes with an increase in the quantum efficiency of the process (Fig. 3, A, curve 2). In the absence of nonlinearity on the initial segment of the curve (Fig. 1, B, curve 1), the enhancement effect is not significant (Fig. 3, A, curve 3). This is clearly seen in Fig. 3, B. The absence of nonlinearity on the initial segment of the curve during light excitation with λ=564 nm and λ=883 nm (Fig. 1, B, curves 3, 4) is accompanied by the absence of the enhancement effect (Fig. 3, B, curves 2, 3).

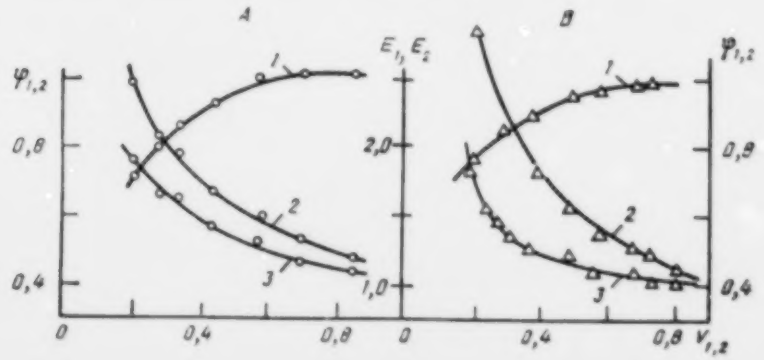

Fig. 2. Curves of relative quantum efficiency and the effect of photosynthetic enhancement in marine macroalgae: A - *Ulva fenestrata*, B - *Punctaria plantaginea*; 1 - relative quantum efficiency ($\phi_{1,2}$); 2 - effect of photosynthetic enhancement for the primary beam (E_1), 3 - for the secondary beam (E_2)

As a result of our investigations and analysis of the literature, we can conclude that the observed effects of enhancement are due entirely to the sigmoid nonlinearity of the photosynthetic light curve. The enhancement effects resulting from the unbalance of the two photosystems of photosynthesis were obviously not observed. The latter

may be due to the fact that the photosynthetic process occurs with the constant overloading of one of the photosystems (most probably the first one).

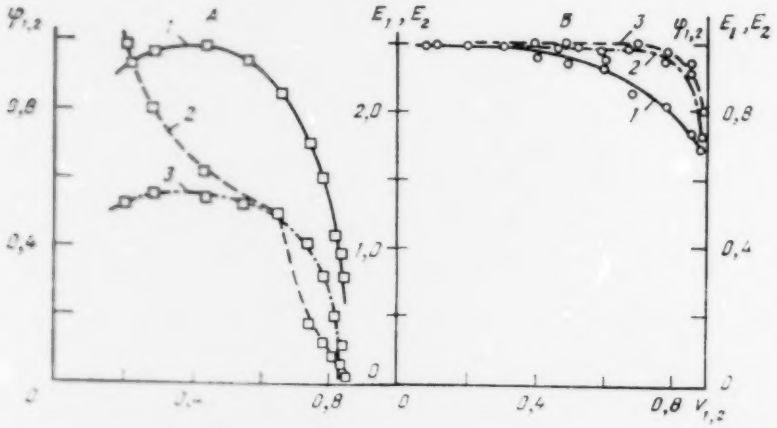

Fig. 3. Curves of the relative quantum efficiency and the effect of photosynthetic enhancement in marine macroalgae of the species *Porphyra yezoensis*: A - from a darkened place (cavern), B - from an illuminated shallow area; 1 - relative quantum efficiency ($\phi_{1,2}$), 2 - effect of photosynthetic enhancement for the primary beam (E_1), 3 - for the secondary beam (E_2)

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